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Cranial infraspecific differentiation in *Proechimys iheringi* Thomas (Rodentia: Echimyidae)

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Abstract

Proechimys iheringi Thomas is an echimyid rodent occurring in eastern Brazil from the states of Bahia to São Paulo. Moojen (1948) recognized six subspecies of *P. iheringi* primarily on the basis of clinal variation in the number of cheekteeth counterfolds. In this study we analyzed infraspecific differentiation in 13 morphometric cranial characters in three populations assignable to three subspecies of *P. iheringi*. Cranial dimensions vary clinally increasing from north to south and morphometric differentiation is correlated with geographic distance. The congruence between the clinal variation in cheekteeth counterfolds and cranial traits indicates that the trinomial nomenclature should not be applied to *P. iheringi*.

Introduction

Proechimys iheringi Thomas is an echimyid rodent which occurs in eastern Brazil, ranging from Bahia to São Paulo (Moojen 1948). In a detailed analysis of infraspecific differentiation in *P. iheringi* Moojen (1948) detected variation in several skull traits including incisive foramen, tympanic bulla, mesopterigoid fossa, palatine foramen, and vomerine sheath. In spite of the variation in these characters, Moojen (1948) relied primarily on the number of cheekteeth counterfolds, which varies clinally increasing from north to south, to recognize six subspecies in *P. iheringi*, namely *P. i. denigratus* from Bahia, *P. i. gratiosus, P. i. paratus*, and *P. i. panema* from Espirito Santo, *P. i. bonafidei* from Rio de Janeiro, and *P. i. iheringi* from São Paulo (Fig. 1). The subspecific structure in *P. iheringi* is thus based on a trait that varies on a cline and whose differentiation is correlated with geographic distance (Moojen 1948).

In this paper, we analyzed cranial variation in three populations of *P. iheringi* assignable to the following subspecies: *P. i. denigratus, P. i. gratiosus, P. i. bonafidei* from the states of Bahia, Espírito Santo, and Rio de Janeiro, respectively. The primary objective of this study was to determine whether the pattern of differentiation in cranial quantitative traits is congruent with the clinal variation in cheekteeth counterfolds and to address the question of recognition of infraspecific units in *P. iheringi*.

Material and methods

A total of 54 specimens of *P. iheringi* available in the mammal collection of the Museu Nacional (Rio de Janeiro) was examined in this study. All specimens were classified to one of the 10 age categories defined by Patton and Rogers (1983) for *P. brevicauda* on the basis of tooth eruption and occlusal surface wear criteria. This procedure was employed in order to control the ontogenetic source of variation, and 42 specimens from age classes 8–10 were selected for the analysis of geographic variation because they were adults by the criteria of Patton and Rogers (1983).

The specimens analyzed in this study represent samples collected at the following localities: Ilhéus, state of Bahia (13° 01′ S, 40° 01′ W; n = 16), Santa Tereza, state of Espírito Santo (19° 55′ S, 40° 36′ W;

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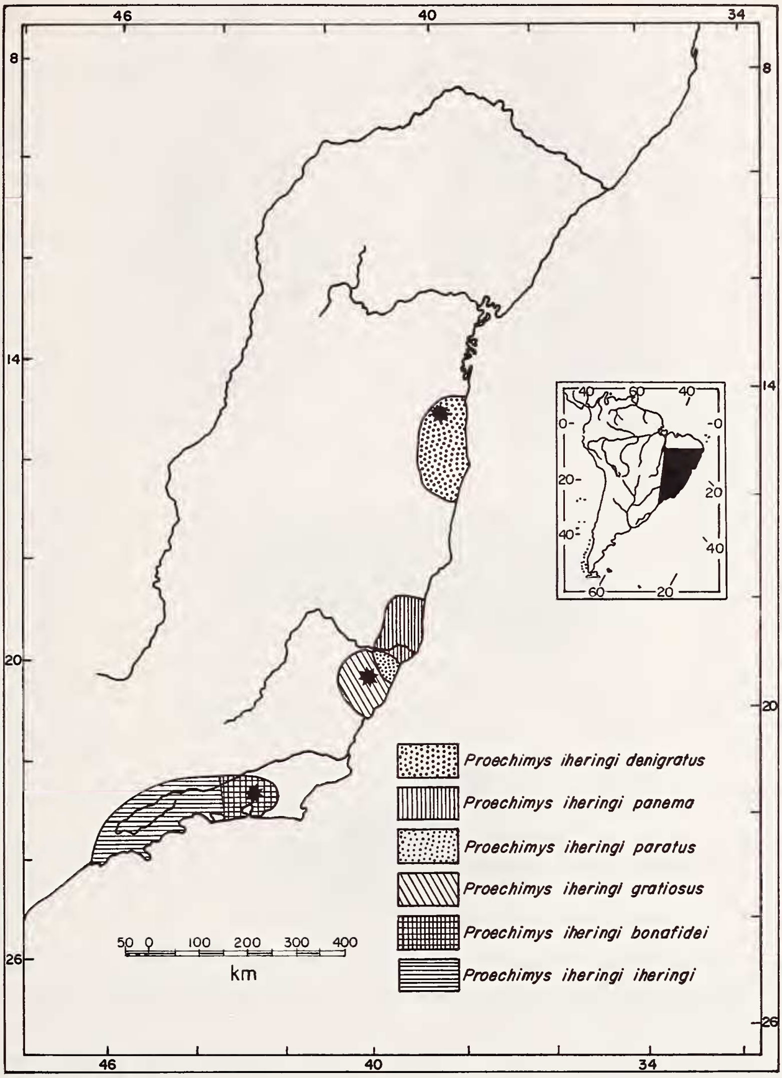

Fig. 1. Ranges for the subspecies of *Proechimys iheringi* Thomas according to Moojen (1948). The stars denote locality samples analyzed in this study

n = 18) and Teresópolos, state of Rio de Janeiro (22° 26′ S, 42° 36′ W; n = 8). Sexes were pooled in the analysis of geographic variation to increase sample sizes.

Twelve cranial measurements defined in Patton and Rogers (1983) in addition to one mandibular measurement were taken with electronic digital calipers accurate to 0.01 mm, as follows: palatal length A (PL), zygomatic breadth (ZB), nasal length (NL), interorbital constriction (IC), rostral breadth (RB), diastema length (DL), rostral depth (RD), skull length (SL), basal length (BL), rostral length (RL), maxillary breadth (MB), pospalatal length (PP), and mandibular length (ML) (Fig. 2).

Cranial character variation in *P. iheringi* was analyzed by univariate and multivariate procedures (Sokal and Rohlf 1981; Neff and Marcus 1980). Cranial characters were tested for significant differences among localities by univariate analysis of variance (anova). Significant characters were tested for maximally non-significant subsets of means employing Ryan-Einot-Gabriel-Welsch (regwf) test on the main effect represented by the variable locality.

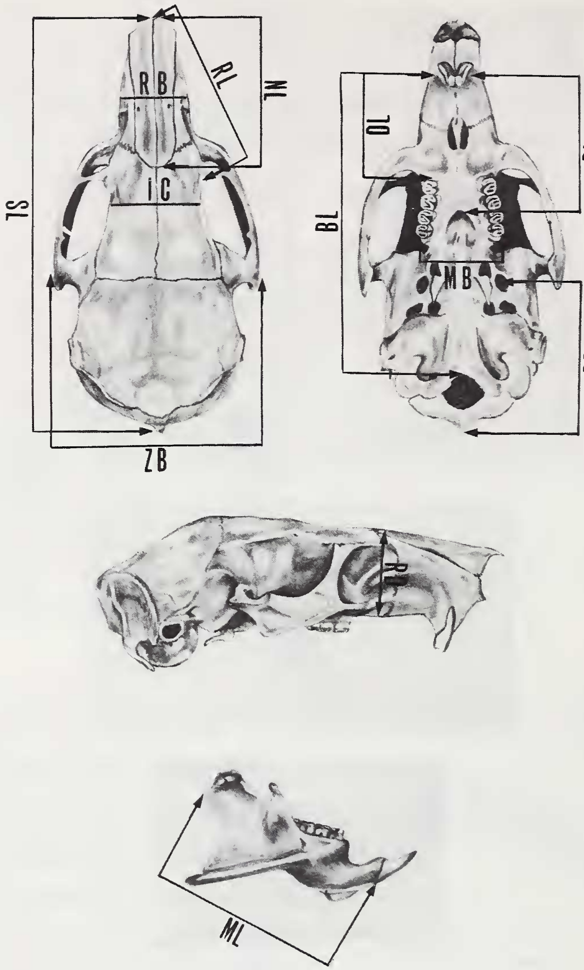

Fig. 2. Thirteen measurements taken on the skulls of *Proechimys iheringi* Thomas (see text for explanation of measurement abbreviations)

The pattern of variation in multivariate character space was analyzed by principal components analysis (Neff and Marcus 1980) and size-independent canonical discriminant analysis (Strauss 1985). The first pooled among-group principal component was used to study size variation among populations of *P. iheringi*. Scores derived from the first principal component were used as a measure of individual overall cranial size and were tested by univariate ANOVA for heterogeneity among the populations.

Size-independent canonical discriminant analysis was employed to analyze patterns of discrimination and ordination among the *P. iheringi* populations. This procedure removes the effect of size variation within groups by performing canonical discriminant analysis on the residuals obtained from the regressions of each log-transformed character separately on the first pooled within-group principal component (Strauss 1985). This procedure was employed because *P. iheringi* shows post-ontogenetic growth (indeterminate growth) that generates size variation within populations (Pessôa 1989) that may confound the analysis of geographic variation (Thorpe 1983). Scores derived from canonical discriminant analysis were plotted to assess the pattern of ordination and discrimination among the populations of *P. iheringi*. Canonical loadings were expressed as bivariate correlations calculated between original character values and scores on the canonical variates (Strauss 1985).

Statistical analyses were performed using SAS-PC Version 6, the current microcomputer edition of the Statistical Analysis System (SAS Institute, 1988).

Results

All cranial characters, except for palatal length and diastema length, increase in mean size from north to south, i.e. from the state of Bahia to the state of Rio de Janeiro (Table 1). Univariate analysis of variance indicates that all cranial traits differ significantly in the three populations of *P. iheringi* (Table 1). Nevertheless, the pattern of inter-locality differentiation in cranial traits is not uniform as indicated by the REGWF procedure (Table 1). Cranial

Table 1. **Standard statistics for 13 cranial characters (in mm) in three populations (BA, ES, and RJ) of *Proechimys iheringi* Thomas**

Character	Mean (SD)	Mean (SD)	Mean (SD)	F	P
Palatal length	ES 15.82 (0.79)	BA 16.30 (0.79)	RJ 16.80 (0.76)	4.35	0.0201
Zygomatic breadth	BA 24.02 (1.21)	ES 25.32 (1.12)	RJ 26.08 (1.18)	9.58	0.0004
Nasal length	BA 15.91 (0.98)	ES 17.47 (0.99)	RJ 19.33 (1.27)	28.41	0.0001
Interorbital constriction	BA 11.06 (0.57)	ES 11.53 (0.96)	RJ 12.47 (0.55)	9.50	0.0005
Rostral breadth	BA 7.03 (0.58)	ES 7.36 (0.58)	RJ 8.26 (0.43)	12.97	0.0001
Diastema length	ES 10.16 (0.80)	RJ 10.98 (0.63)	BA 11.15 (0.78)	7.38	0.0020
Rostral depth	BA 9.36 (0.52)	ES 10.05 (0.83)	RJ 10.87 (0.63)	13.21	0.0001
Skull length	BA 46.27 (1.81)	ES 49.89 (2.31)	RJ 53.00 (2.66)	26.87	0.0001
Basal length	BA 34.74 (1.67)	ES 34.84 (1.55)	RJ 37.22 (1.57)	7.30	0.0022
Rostral length	BA 19.39 (0.99)	ES 21.43 (1.71)	RJ 23.28 (1.35)	22.26	0.0001
Maxillary breadth	BA 8.17 (0.42)	ES 8.45 (0.88)	RJ 9.09 (0.51)	5.28	0.0096
Pos-Palatal length	BA 2.72 (0.75)	ES 23.40 (0.94)	RJ 24.58 (1.26)	27.20	0.0001
Mandibular length	BA 23.87 (1.23)	ES 24.70 (1.38)	RJ 26.20 (1.54)	7.87	0.0014

Statistics given are mean, standard deviation, F-value of an analysis of variance and associated probability levels (P), and results of REGWF analysis. Lines below population means connect nonsignificant subsets. BA = Bahia, ES = Espirito Santo, and RJ = Rio de Janeiro.

characters such as interorbital constriction, rostral breadth, basal length, maxillary breadth, and mandibular length are not significantly different in the populations of Bahia and Espírito Santo, although individuals in both populations are significantly smaller than those in the population from Rio de Janeiro. The three populations differ statistically in several cranial traits including nasal length, rostral depth, skull length, rostral length, and pos-palatal length. Palatal length, zygomatic breadth, and diastema length have unique patterns of variation among the three populations (Table 1).

In order to analyze size variation among populations of *P. iheringi* in multivariate character space, the first pooled among-group principal component (PAGPC-1) was extracted from the covariance matrix of log-transformed character values. PAGPC-1 can be interpreted as a general size factor since all vector coefficients are positive and have significant correlations with log-transformed character values (Strauss 1985) (Table 2). The scores from principal components analysis for the individuals in the three populations of *P. iheringi* can then be used as a measure of multivariate cranial size. Mean score values increase from north to south in the populations of Bahia (−0.0729), Espírito Santo (0.0056), and Rio de Janeiro (0.1163) and these mean values were shown to be highly significant different by an univariate ANOVA ($F = 16.48$; $P < 0.0001$).

The pattern of ordination and discrimination of *P. iheringi* populations was assessed by

Table 2. **Principal component and canonical variate loadings for 13 cranial morphometric characters in *Proechimys iheringi* Thomas**

Character	PAGPC-1	r	CV-1	CV-2
Palatal length	0.160	0.709**	0.845**	0.067ns
Zygomatic breadth	0.212	0.852**	−0.083ns	−0.416*
Nasal length	0.380	0.935**	−0.650**	0.238ns
Interorbital constriction	0.134	0.935**	−0.652**	0.205ns
Rostral breadth	0.339	0.816**	−0.053ns	0.341*
Diastema length	0.178	0.510*	0.966**	0.002ns
Rostral depth	0.357	0.932**	−0.253ns	−0.116ns
Skull length	0.285	0.952**	−0.764**	−0.078ns
Basal length	0.193	0.846**	0.590**	0.201ns
Rostral length	0.401	0.960**	−0.709**	−0.132ns
Maxillary breadth	0.306	0.798**	0.211ns	−0.050ns
Pos-Palatal length	0.242	0.889**	−0.667**	−0.045ns
Mandibular length	0.247	0.900**	0.349*	−0.153ns
Percent of variance explained	73.71		89.79	10.21

Canonical variate loadings are expressed as vector correlations between log-transformed character values and canonical scores. PAGPC-1 is the pooled among-group first principal component. r is the Pearson product-moment correlation coefficient between cranial characters and the first principal component. * P < 0.05; ** P < 0.0001; n = non significant

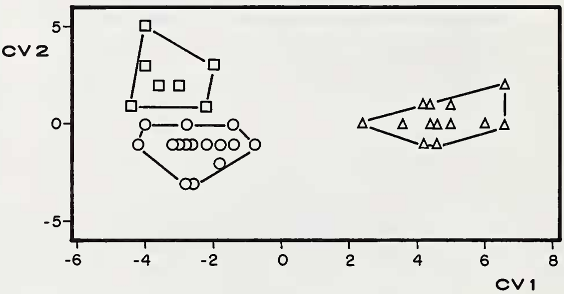

Fig. 3. Scatterplot of individual scores from a size-independent canonical discriminant analysis from three populations of *Proechimys iheringi*. Bahia (triangles), Espírito Santo (circles), and Rio de Janeiro (squares)

size-independent canonical discriminant analysis. The first canonical variate (CV-1) explains 89.79 % of the total among-group variation while CV-2 accounts for the remaining 10.21 %. The plot of canonical variate scores shows that the three populations of *P. iheringi* occupy different positions in the reduced space of canonical variates (Fig. 3). The population from Bahia is discriminated from the populations from Espírito Santo and Rio de Janeiro along CV-1, whereas individual scores for the latter populations have non-overlapping distributions along CV-2. Figure 3 also indicates that the populations from Espírito Santo and Rio de Janeiro, which are the geographically closest, are also morphometrically more similar. These populations are more differentiated morphometrically from the population of Bahia which is geographically farther.

The vectors of correlations between canonical variates and original log-transformed character values indicate that the population from Bahia differs from those of Espírito Santo and Rio de Janeiro in most cranial measures of length (Table 2). Canonical variate 1 correlations indicate a contrast between palatal length, diastema length, basal length, and mandibular length with positive significant correlations and nasal length, interorbital constriction, skull length, rostral length, and pos-palatal length with negative significant correlations. On the other hand, the population from Espírito Santo differs from that of Rio de Janeiro in zygomatic breadth with a negative significant correlation and rostral breath with a positive significant correlation (Table 2).

Discussion

The univariate statistical analysis of cranial character variation did not produce a consistent pattern of inter-locality population differentiation in *P. iheringi*, although most characters vary in a cline increasing in size from north to south. The lack of consistency in character trends observed for *P. iheringi* in this study is a common result, whenever morphometric characters are analyzed univariately (Baker 1980; Thorpe 1983; Macêdo and Mares 1987).

The multivariate procedures employed produced a much clearer picture of the nature and extent of inter-locality differentiation in *P. iheringi*. Multivariate cranial size, estimated by mean score values derived from principal components analysis, increases from north to south confirming the cline observed for most cranial morphometric traits in *P. iheringi* in the univariate analysis. This cline follows the same direction of the gradient in cheekteeth counterfolds observed by Moojen (1948). The pattern of ordination of *P. iheringi* populations in the space of canonical variates further indicates a correlation between morphometric and geographic distance confirming Moojen's (1948) observations based on qualitative arguments.

The analysis of geographic differentiation in *P. iheringi* reported in this paper is based upon population samples representing three subspecies among the six forms recognized by Moojen (1948). We believe nevertheless that our findings are representative of the overall pattern of variation in *P. iheringi* since the three subspecies we analyzed are distributed over most of the range of this species (Fig. 1). Our results, in addition to Moojen's (1948) findings, indicate that the variation in *P. iheringi* is geographically structured in a cline of increasing cranial dimensions and number of cheekteeth counterfolds from northern to southern populations. The recognition of subspecies on the basis of clinal variation, as is the case for *P. iheringi*, has been criticized primarily due to the continuous nature of the variation expressed in a cline (Barrowclough 1982; Thorpe 1987). The validity of the recognition of subspecific units in *P. iheringi* can be questioned since the application of trinomials has been considered suitable to describe character variation that do not simply form clines but rather diagnoses groups of populations indicating the existence of independent infraspecific units (Barrowclough 1982; Thorpe 1987; Smith and Patton 1988; Patton and Smith 1989).

Our preliminary study indicates that, on the basis of the pattern of cranial variation, the use of the subspecific nomenclature is not justified for *P. iheringi*. Nevertheless, other character systems should be surveyed to assess the nature and structure of variation in order to understand the process of differentiation in this species and determine whether independent evolutionary units (sensu Smith and Patton 1988; Patton and Smith 1989) should be recognized for *P. iheringi*.

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Zusammenfassung

Intraspezifische Schädelvariabilität bei Proechimys iheringi Thomas (Rodentia: Echimyidae)

Schädel von Igelratten *(Proechimys iheringi)* aus drei Populationen, die drei der sechs beschriebenen Unterarten dieser Art zuzuordnen sind, wurden in 13 Maßen verglichen. Danach nimmt die Schädelgröße von Norden nach Süden zu. Die allgemeinen morphometrischen Abstände zwischen den Populationen sind mit ihren geographischen Abständen korreliert. Da sich auch die Zahl der Schmelzfalten in gleicher Richtung klinal ändert, läßt sich eine Gliederung von *Proechimys iheringi* in Unterarten mit diesen Merkmalen nicht rechtfertigen.

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